

Freshwater mussels (Bivalvia: Unionidae) in the Verdigris, Neosho, and Spring River basins of Kansas and Missouri, with emphasis on species of concern

Brian K. Obermeyer^{1*}, David R. Edds¹, Carl W. Prophet¹, and Edwin J. Miller²

¹Division of Biological Sciences, Emporia State University, Emporia, Kansas 66801, U. S. A.

²Kansas Department of Wildlife and Parks, P. O. Box 945, Independence, Kansas 67301, U. S. A.

Abstract: We examined freshwater mussel assemblages at 99 sites from 1993 to 1995 in the Arkansas River system of southeastern Kansas and southwestern Missouri. Emphasis was placed on assessing the distribution, relative abundance, and habitat use of five unionid candidates for future federal listing (species of concern): *Lampsilis rafinesqueana* Frierson, 1927, *Ptychobranthus occidentalis* (Conrad, 1836), *Cyprogenia aberti* (Conrad, 1850), *Quadrula cylindrica* (Say, 1817), and *Alasmidonta marginata* Say, 1818. We collected a total of 15,068 mussels of 35 species, including 1,301 *L. rafinesqueana*, 83 *P. occidentalis*, 29 *C. aberti*, seven *Q. cylindrica*, and one *A. marginata*. The three most abundant species collected from our study were *Amblema plicata* (Say, 1817), *Q. metanevra* (Rafinesque, 1820), and *Q. pustulosa* (Lea, 1831). However, species abundance rankings varied from stream to stream; for example, *L. rafinesqueana* was the most abundant species collected in the Spring River. Habitat use by candidate species varied considerably between streams, however, they were consistently found in shallow riffles and runs (mean depths 25.0-33.7 cm), with stable and moderately compacted substratum, predominantly gravel, with a minimum of silt.

Key Words: Unionidae, species of concern, freshwater mussels, Arkansas River system

Prompted by concern for diminishing freshwater mussel populations, the U. S. Fish and Wildlife Service (USFWS) listed six unionid species native to the Arkansas River system of southeastern Kansas and southwestern Missouri as candidates ("Category 2") for possible addition to the list of U. S. Endangered and Threatened Wildlife (15 November 1996, *Federal Register* 59(219):58982-59028). [Note: USFWS has discontinued the listing of "Category 2" candidate species, and has since labeled them as species of concern (05 December 1996, *Federal Register* 61:64481-64485)]. These species of concern are the Neosho mucket (*Lampsilis rafinesqueana* Frierson, 1927), Ouachita kidneyshell [*Ptychobranthus occidentalis* (Conrad, 1836)], western fanshell [*Cyprogenia aberti* (Conrad, 1850)], rabbitsfoot [*Quadrula cylindrica* (Say, 1817)], elktoe (*Alasmidonta marginata* Say, 1818), and purple lilliput [(*Toxolasma lividus* (Rafinesque, 1831)].

Lampsilis rafinesqueana is endemic to the Arkansas River system (Neosho, Spring, Elk, Illinois, and Verdigris River basins) in Kansas, Missouri, Oklahoma, and Arkansas (Gordon and Brown, 1980; Johnson, 1980; Oesch, 1984; Harris and Gordon, 1987; Mather, 1990;

Stewart, 1992; Obermeyer *et al.*; 1995; Clarke and Obermeyer, 1996). Although populations of *L. rafinesqueana* persist within these states, its range has declined (Cope, 1979; Metcalf, 1980; Mather, 1990; Stewart, 1992; Clarke and Obermeyer, 1996; Obermeyer *et al.*, 1995, 1997). *Ptychobranthus occidentalis* is confined to the Arkansas, Black, Red, St. Francis, and White River systems in Arkansas, Kansas, Missouri, and Oklahoma (Valentine and Stansbery, 1971; Johnson, 1980). Although Buchanan (1980) and Oesch (1984) reported *P. occidentalis* in the Meramec River basin of Missouri (*i.e.* Upper Meramec River near the mouth of Blue Springs Creek), both (A. C. Buchanan, pers. comm.; R. D. Oesch, pers. comm.) have discounted this locality account due to suspected specimen mislabeling. *Cyprogenia aberti* is native to the Arkansas, Black, St. Francis, Ouachita, and White River systems in Arkansas, Kansas, Missouri, and Oklahoma (Johnson, 1980; Oesch, 1984; Harris and Gordon, 1987; Stewart, 1994). Its previously reported presence in the Meramec River basin of Missouri (*e.g.* Buchanan, 1980; Oesch, 1984) is now considered in error due to the same suspected mislabeling of specimens mentioned for *P. occidentalis*. *Cyprogenia aberti* is currently found in 14 streams in Arkansas, five in Missouri, and three

*Present address: Rt. 2, Box 141, Eureka, Kansas 67045, U. S. A.

in Kansas (Stewart, 1994); it is considered extirpated in Oklahoma (Mather, 1990). *Quadrula cylindrica* is native to the Ozarkian and Cumberland faunal regions (Johnson, 1980) of 13 states (Williams *et al.*, 1993), perhaps reaching its greatest abundance in the Black River system of Arkansas (D. H. Stansbery, pers. comm.). A subspecies, *Q. cylindrica strigillata* (Wright, 1898), which is considered by some as an ecomorph (*e.g.* Simpson, 1914; Gordon and Layzer, 1989; Clarke and Obermeyer, 1996) (but see Ortmann, 1920), occurs in the Clinch, Powell, and Holston Rivers of the Upper Tennessee River drainage (Ortmann, 1920; Bogan and Parmalee, 1983; Yeager and Neves, 1986). *Alasmidonta marginata* is widely distributed throughout eastern North America, being found in 22 states and one Canadian province (Clarke, 1981; Williams *et al.*, 1993). *Toxolasma lividus* is found in the Ohioan, Cumberlandian, and Ozarkian faunal regions (Johnson, 1980) of 12 states (Williams *et al.*, 1993).

The primary objectives of this study were to assess the distribution, abundance, and habitat use of five of the six species of concern mentioned above (*i.e.* all except *Toxolasma lividus*) in the Arkansas drainage system in eastern Kansas and southwestern Missouri (Neosho, Verdigris, and Spring River basins). However, we also noted the composition of the total mussel assemblage.

STUDY AREA

The Neosho and Verdigris River basins are situated within the tallgrass prairie ecoregion in southeastern Kansas. Cross and Collins (1995) termed the lotic waters of these two basins as Ozark-border streams, and characterized them as having the greatest habitat diversity for fishes in Kansas. The greatest richness of Kansas' unionid fauna also occurs within these basins – 37 species (Obermeyer *et al.*, 1997). Both basins are primarily agricultural, with native rangeland in many headwater reaches, whereas extensive cultivation occurs on and near the flood plains of tailwater reaches. Chert-gravel, derived of Permian and Pennsylvanian limestones (Wilson, 1984; Aber, 1992), is the dominant substratum of shallow riffle habitats. Principal streams of the Neosho and Verdigris River basins along with their respective drainage area (km²) in Kansas follow: the Neosho (15,000) and Cottonwood (4,940) Rivers of the Neosho River basin, and the Verdigris (8,690), Fall (2,290), and Elk (1,820) Rivers in the Verdigris River basin (Fig. 1). Despite their size, these streams are subject to periodic flow interruptions during severe droughts (Deacon, 1961; Geiger *et al.*, 1995; Miller and Obermeyer, 1997). Recent flow disruptions have resulted from the construction and operation of several federal flood-control impoundments: Council Grove Lake and John

Redmond Reservoir (Neosho River), Marion Lake (Cottonwood River), Fall River Lake (Fall River), Toronto Lake (Verdigris River), and Elk City Lake (Elk River) (Fig. 1).

Streams in the Spring River basin (Fig. 1), excluding the North Fork Spring River, which is a prairie stream (Davis and Schumacher, 1992), originate from the northwestern flank of the Ozark Uplift. The basin's flow is generally westward until reaching Kansas, where it turns southward into Oklahoma (Davis and Schumacher, 1992), eventually joining the Neosho River. The Spring River basin drains approximately 5,415 km² of southwestern Missouri, and an additional 1,370 km² in southeastern Kansas (Davis and Schumacher, 1992). Streams examined in the Spring River basin included the Spring and North Fork Spring Rivers, and Shoal and Center Creeks. These streams differ from Ozark-border streams by having lower turbidity, richer aquatic faunas (Cross and Collins, 1995), and flows sustained by headwater springs during droughts. Land use in several of these streams also differs from that in the Neosho and Verdigris basins in that a sizable proportion of the drainage area is forested (*e.g.* 45% for Shoal Creek; Davis and Schumacher, 1992). In addition, extensive lead and zinc mining has occurred in the Spring River basin, which has especially affected the lower Spring River and Shoal Creek in Kansas and Center Creek in Missouri (Kansas Department of Health and Environment, 1980; Davis and Schumacher, 1992). Furthermore, these streams lack the large flood-control impoundments that have altered streams in the Neosho and Verdigris basins (Obermeyer *et al.*, 1997). The mussel assemblage of the Spring River basin differs from that of the Neosho and Verdigris River basins in having the following species: *Alasmidonta marginata*, *A. viridis* (Rafinesque, 1820), *Fusconaia ozarkensis* (Call, 1887), *Toxolasma lividus* (Rafinesque, 1831), and *Venustaconcha ellipsiformis* (Conrad, 1836) (Gordon and Brown, 1980; Cope, 1985; Obermeyer *et al.*, 1995). Also, four species present in the latter basins are absent from the Spring River basin: *Ellipsaria lineolata* (Rafinesque, 1820), *Truncilla donaciformis* (Lea, 1827), *T. truncata* Rafinesque, 1820, and *Megaloniais nervosa* (Rafinesque, 1820) (Cope, 1985; Obermeyer *et al.*, 1995).

METHODS

SAMPLING

Sampling sites were confined to streams in the Arkansas River Basin with known accounts of one or more of the targeted species. An attempt was made to space sample sites evenly within each stream; however, unsuitable habitat in some stream stretches (*e.g.* unstable banks, bedrock substratum) and/or difficulty in securing legal access sometimes made this impossible. We also tried to

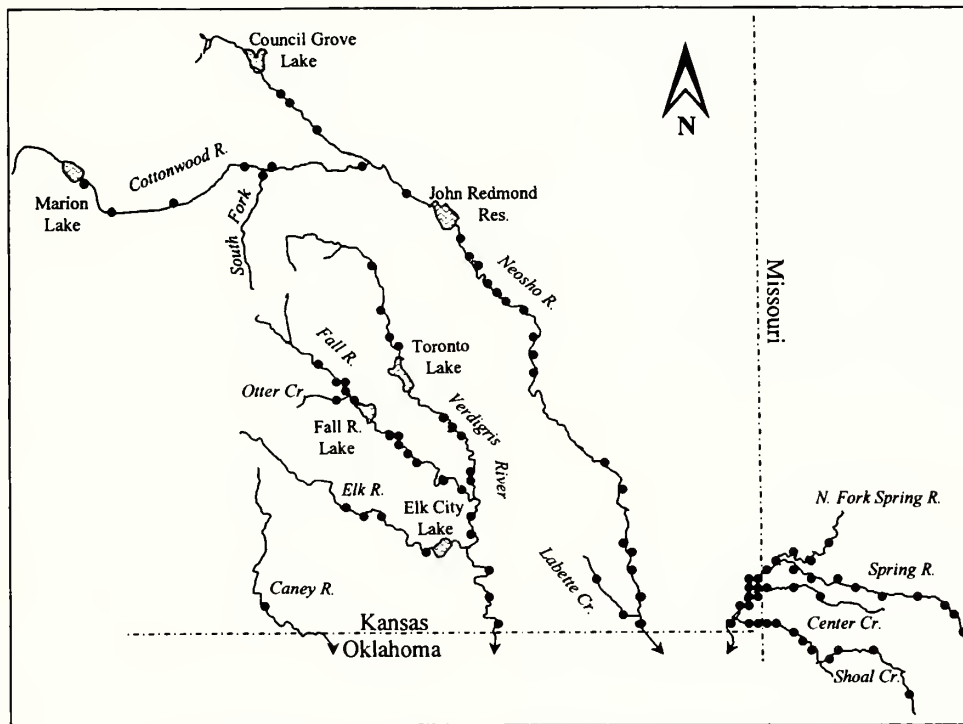


Fig. 1. Sampling sites in southeastern Kansas and southwestern Missouri.

sample sites examined by previous surveyors; unfortunately, many of these sites lacked exact locality data.

To locate living mussels in shallow water (15 cm to < 1 m) with adequate visibility, we used a snorkel and face mask, whereas at depths exceeding 1 m, SCUBA was used. Mussels were located both by tactile cues (groping) and by visual cues during snorkeling and SCUBA searches. We also visually searched for mussels in shallow habitats as well as recently exposed substratum. Sampling was concentrated in riffles and runs; however, runs and pools were also examined to assess usage of these habitats. All searches were timed to quantify sampling effort, which ranged from 40 min to 9 h, depending on quantity and quality of habitat. Weather conditions and water levels also influenced sampling effort.

We also quantitatively examined 14 sites in Kansas (Neosho = 9, Spring = 2, Fall = 3) using a 1-m² quadrat; a total of 505 quadrats was sampled at these sites. Quadrats were placed along measured coordinates chosen randomly, with the substratum excavated by hand to an approximate depth of 10-15 cm.

To seek evidence of young recruits, we sampled substratum from habitats cited as being most often utilized by juveniles (Isely, 1911; Clarke, 1986; Neves and Widlak, 1987); substratum was dredged with a shovel and transferred to a 1-m² sieve (6-mm mesh) supported by a floating 15-cm PVC-pipe frame. Dredging ceased when the weight

of the substratum caused the frame to sink. The substratum was then sieved in an attempt to locate small mussels. The number of sieve samples examined at each site varied from 0 to 21.

Except for a few specimens collected for reference, living unionids were identified in the field, measured with either a dial caliper or an aluminum plate shell-sizer with openings of 2, 3, 4, 6, 8, 10, and 12 cm (Obermeyer, 1996a), and returned to their original location. Reference shells from sites sampled in 1994 are deposited in the Ohio State University Museum of Zoology in Columbus, Ohio, and vouchers from 1995 sites will be housed at the Kansas Biological Survey, University of Kansas, Lawrence. Nomenclature of unionids follows Turgeon *et al.* (1988); however, subgenera *Utterbackia* Baker, 1927, and *Pyganodon* Crosse and Fischer, 1893, are elevated to generic status following Hoeh (1990), and *Fusconaia ozarkensis* and *F. flava* (Rafinesque, 1820) collected from the Spring River and Shoal Creek are listed as *Fusconaia* spp. due to identification uncertainties. Nomenclature of fishes follows Robins *et al.* (1991).

HABITAT CHARACTERIZATION

At specific locales where living individuals of candidate species were found, we made visual estimates of three substratum variables: substratum compaction, percent composition of substratum types, and silt deposition on the

substratum. Substratum compaction was coded as 0, 1, or 2, with 0 being loose, 1 moderately compacted, and 2 very compacted. Substrata were divided into five approximate size classes: mud (< 0.8 mm), sand (0.8 - 4 mm), gravel (4 - 50 mm), cobble (50 - 290 mm), and boulder (> 290 mm) (modified from Platts *et al.*, 1983). We coded the degree of silt deposition from 0 to 3, where 0 characterized a clean substratum, 1 had a detectable silt layer, 2 was moderately covered with silt, and 3 was heavily silt-laden. Current speed and water depth were measured for each candidate specimen with a pygmy Gurley current meter no. 625 at 60% depth and at the substratum-water interface (100% depth).

RESULTS

From a combined effort of 505 1-m² quadrats and approximately 200 h of qualitative sampling from 99 sites in the Arkansas River system (Neosho River basin = 30 sites; Verdigris River basin = 32 sites; Spring River basin = 37 sites), we collected 15,068 living mussels representing 35 species (Table 1). *Corbicula fluminea* (Müller, 1774), a recent bivalve invader (Corbiculidae), was also found in all streams. Over 9% of our collections consisted of species of concern, with 1,301 *Lampsilis rafinesqueana*, 83 *Ptychobranhus occidentalis*, 29 *Cyprogenia aberti*, seven *Quadrula cylindrica*, three *Toxolasma lividus*, and one *Alasmidonta marginata* collected. The most abundant species encountered during the survey was *Amblema plicata* (Say, 1817), comprising 18.9% of the total sample, followed by *Quadrula metanevra* (Rafinesque, 1820) and *Q. pustulosa* (Lea, 1831), representing 18.2% and 11.8%, respectively (Table 1). However, species rank varied among basins and streams; *Q. metanevra*, *A. plicata*, and *Q. pustulosa* were the three most common species in the Neosho River Basin, *A. plicata*, *Q. pustulosa*, and *Q. metanevra* the most numerous in the Verdigris River basin, and *L. rafinesqueana*, *Fusconaia* spp., and *Elliptio dilatata* (Rafinesque, 1820) the most common in the Spring River basin (Table 1).

Although *Lampsilis rafinesqueana* was the fourth most abundant species encountered in this study (8.6% of total sample), most of these individuals (1192 = 91.6%) were collected from the Spring River, representing 40.2% of the Spring River total (Table 1). This species was found alive at 13 of 20 Spring River sites, from just downstream of state Highway 97 bridge near Stott City, Lawrence County, Missouri, to the confluence of Turkey Creek, Kansas (Fig. 2). It was the most abundant species encountered at 11 of these sites. In Shoal Creek, 26 *L. rafinesqueana* were collected at five of 11 sites (Table 1; Fig. 2), but only in the Missouri portion of this stream. Two

of three North Fork Spring River sites yielded 12 *L. rafinesqueana* specimens (Table 1; Fig. 2). This species was not collected alive in Center Creek, but one recently dead specimen was recovered. In the Neosho River, 32 *L. rafinesqueana* were collected at six of 21 sites, representing 0.6% of this river's collection (Table 1); these were all found downstream from John Redmond Reservoir (Fig. 2). In the Verdigris River, a total of five *L. rafinesqueana* was found at four of 14 sites (0.2% of the total Verdigris River sample; Table 1); all four of these sites were located downstream from Toronto Lake and upstream from the confluence of the Elk River (Fig. 2). Thirty-four *L. rafinesqueana* were collected at five of 12 Fall River sites between Fall River Lake and the confluence of the Verdigris River (Table 1; Fig. 2), representing 1.7% of the total sample from this stream. Although weathered shells of this species were observed at sites in the Cottonwood, Caney, and Elk Rivers, living or recently dead specimens were not found (Table 1).

Young *Lampsilis rafinesqueana*, either living or freshly dead, were found at few sites. Based on external estimations of annuli, most Verdigris and Neosho basin specimens were over 20 years old; only three specimens collected in these two basins were estimated to be of young age (6-10 years). Spring River basin specimens were comprised mostly of two or three cohorts between eight and 20 years of age; the youngest *L. rafinesqueana* specimens collected alive or as recently dead specimens were four years old, the smallest being a recently dead specimen from Shoal Creek that measured 49 x 32 x 16 mm (length, height, and width, respectively). In the Neosho and Verdigris River basins, mean length for caliper-measured *L. rafinesqueana* was 131.2 mm (SD = 12.96), with specimens ranging 94 - 163 mm. Spring River *L. rafinesqueana*, which were measured with the aluminum shell-sizer, averaged 110.8 mm (SD = 11.10), whereas caliper-measured Shoal Creek specimens were considerably smaller (mean = 72.5 mm, SD = 8.73).

Lampsilis rafinesqueana was collected most often in shallow riffles and runs having predominantly gravel substratum (Table 2); however, there was a substantial difference in habitat use by *L. rafinesqueana* in the Spring River and Shoal Creek compared to that in the Neosho, Fall, and Verdigris Rivers (Table 2). For instance, mean current speed at locales utilized by *L. rafinesqueana* was much higher in the Spring River basin than in prairie streams (Table 2). The mean coded value for silt deposition at *L. rafinesqueana* sites in the Spring River was 0.2 (SD = 0.40) compared to 1.4 (SD = 0.50) in the Neosho, Verdigris, and Fall Rivers (Table 2). These data are likely variant due to the uniqueness of the Spring River compared to other Kansas streams (Cross and Collins, 1995), and because of greater *L. rafinesqueana* densities in the Spring

Table 1. Unionid mussels collected in 1993-1995 from the Neosho, Spring, and Verdigris River basins in southeastern Kansas and southwestern Missouri, and the contribution of each stream. [d, dead (recent); Lr, literature record; wd, weathered dead].

Species	Streams & No. sites:					Neosho Basin				Spring Basin			Verdigris Basin			
	Neosho		S. Fork		Labette	Spring R.	N. Fork Spring R.	Center Cr.	Shoal Cr.	Verdigris R.	Fall R.	Elk R.	Otter Cr.	Caney R.		
	R.	Cwd.	R.	Cwd.	Cr.											
Totals	21	6	1	2	20	3	3	11	14	12	4	1	1			
<i>Alasmidonta marginata</i> Say, 1818	1	-	-	-	1	-	-	wd	-	-	-	-	-			
<i>A. viridis</i> (Rafinesque, 1820)	1	-	-	-	d	-	-	1	-	-	-	-	-			
<i>Ambleria plicata</i> (Say, 1817)	2844	1274	d	91	94	132	wd	47	688	461	57	d	d			
<i>Cyprogenia aberi</i> (Conrad, 1850)	29	Lr	-	-	13	-	-	-	11	5	wd	-	Lr			
<i>Ellipsaria lineolata</i> (Rafinesque, 1820)	87	80	-	-	Lr	-	-	-	7	Lr	-	-	-			
<i>Elliptio dilatata</i> (Rafinesque, 1820)	539	179	d	-	280	23	1	56	Lr	217	51	wd	d			
<i>Fusconaia flava</i> (Rafinesque, 1820)	860	334	1	12	26	26	-	-	219	-	-	-	-			
<i>Fusconaia</i> spp.*	440	-	-	-	372	-	d	68	-	-	-	-	-			
<i>Lampsilis cardium</i> (Rafinesque, 1820)	499	103	d	-	54	27	13	54	106	128	14	d	d			
<i>L. rafinesqueana</i> Frierson, 1927	1301	32	wd	Lr	1192	12	d	26	5	34	wd	-	wd			
<i>L. siliquioidea</i> (Barnes, 1823)	23	Lr	-	-	8	12	2	Lr	wd	d	wd	wd	1			
<i>L. teres</i> (Rafinesque, 1820)	71	16	d	5	1	7	-	Lr	16	20	6	wd	wd			
<i>Lasmsgonia complanata</i> (Barnes, 1823)	151	14	d	16	3	3	-	-	78	29	8	d	d			
<i>L. costata</i> (Rafinesque, 1820)	31	3	wd	-	28	wd	wd	-	wd	wd	wd	Lr	Lr			
<i>Leptodea fragilis</i> (Rafinesque, 1820)	172	113	6	3	Lr	-	-	-	24	23	3	d	d			
<i>Ligumia recta</i> (Lamarck, 1819)	wd	wd	wd	-	wd	-	-	wd	wd	wd	wd	wd	Lr			
<i>L. subrostrata</i> (Say, 1831)	18	d	d	2	2	1	-	9	wd	4	d	d	d			
<i>Megalonia nervosa</i> (Rafinesque, 1820)	209	198	wd	-	Lr	-	-	-	133	47	9	-	-			
<i>Obliquaria reflexa</i> Rafinesque, 1820	490	292	d	9	wd	-	-	-	47	9	wd	wd	-			
<i>Pleurobema coccineum</i> (Conrad, 1834)	421	30	wd	-	335	-	wd	7	40	9	wd	wd	-			
<i>Potamilus ohioensis</i> (Rafinesque, 1820)	5	3	d	-	-	-	-	-	2	-	d	-	d			
<i>P. purpuratus</i> (Lamarck, 1819)	183	103	d	6	1	-	-	-	29	23	20	d	d			
<i>Ptychobranchus occidentalis</i> (Conrad, 1836)	83	wd	wd	-	45	2	-	6	11	19	wd	wd	wd			
<i>Pyganodon grandis</i> (Say, 1829)	14	2	d	1	2	2	d	d	d	7	d	wd	d			
<i>Quadrula cylindrica</i> (Say, 1817)	7	2	wd	-	5	-	-	wd	wd	wd	-	-	-			
<i>Q. metanevra</i> (Rafinesque, 1820)	2748	1786	wd	-	15	-	-	1	658	288	d	-	-			
<i>Q. nodulata</i> (Rafinesque, 1820)	42	12	Lr	wd	Lr	-	-	1	24	6	-	-	-			
<i>Q. pustulosa</i> (L. Lea, 1831)	1779	537	5	30	243	13	wd	d	388	485	78	d	d			
<i>Q. quadrula</i> (Rafinesque, 1820)	683	274	18	53	60	34	-	wd	130	84	29	d	d			
<i>Sirophius undulatus</i> (Say, 1817)	162	7	d	-	14	68	1	2	35	24	11	wd	d			
<i>Toxolasma lividus</i> (Rafinesque, 1831)	3	-	-	-	-	-	-	3	-	-	-	-	-			
<i>T. parvus</i> (Barnes, 1823)	3	Lr	-	-	-	-	-	Lr	1	1	-	-	1			
<i>Tritogonia verrucosa</i> (Rafinesque, 1820)	893	354	29	16	76	33	-	-	160	189	35	1	d			
<i>Truncilla donaciformis</i> (L. Lea, 1828)	62	25	d	d	-	-	-	-	8	29	d	-	Lr			
<i>T. truncata</i> Rafinesque, 1820	6	d	wd	-	Lr	-	-	-	6	wd	wd	-	d			
<i>Unionerius tetralasmus</i> (Say, 1831)	d	d	-	-	-	-	-	Lr	Lr	-	wd	-	Lr			
<i>Utterbackia imbecillis</i> (Say, 1829)	d	Lr	-	-	-	-	-	d	Lr	d	-	-	d			
<i>Venustachoncha ellipsiformis</i> (Conrad, 1836)	208	-	-	-	120	61	7	20	-	-	-	-	-			
Totals	15068	5773	59	2	244	2964	24	300	2787	2135	321	1	2			

**Fusconaia* spp. represents the *Fusconaia flava* (Rafinesque, 1820) and *F. ozarkensis* (Call, 1887) complex.

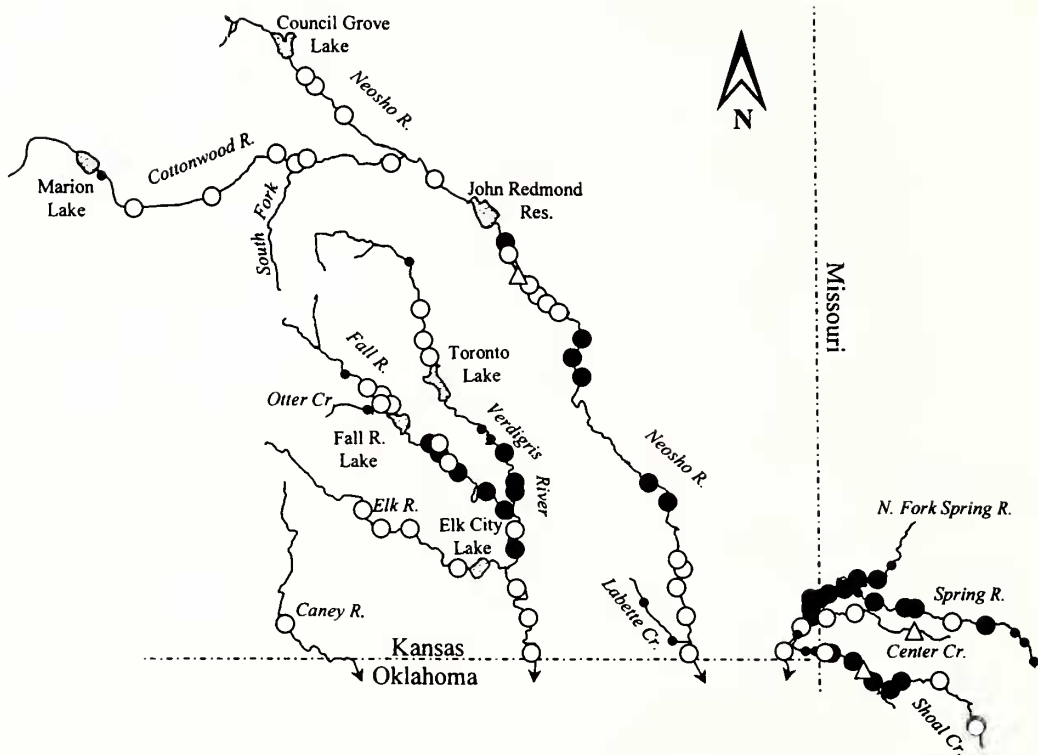


Fig. 2. Range map of *Lampsilis rafinesqueana* in the Neosho, Spring, and Verdigris River basins in southeastern Kansas and southwestern Missouri. Solid circles indicate sites where living specimens were found, triangles represent recently dead specimens, open circles are sites yielding only weathered and/or relic valves, and small solid dots represent sites in which we did not find evidence of the species.

River. For example, 67 *L. rafinesqueana* were collected in one 1-m² quadrat (located at a depth of 28 cm with current speeds of 90 and 68 cm/s at 60 and 100% depth, respectively, in clean, moderately loose substratum consisting of 10% sand, 80% gravel, and 10% cobble); whereas the species was found only sporadically in other Kansas streams.

Ptychobranthus occidentalis ranked nineteenth in relative abundance from collections in the three basins (Table 1). This species was not collected alive in the Neosho River, despite abundant weathered valves at several sites. In the Verdigris River, 11 *P. occidentalis* were found at four sites (Table 1; Fig. 3), representing 0.4% of this stream's total sample. Nineteen specimens were collected at six Fall River sites (Table 1; Fig. 3), comprising 0.9% of unionids collected in this stream. In the Spring River, we collected 45 *P. occidentalis* at ten sites, representing 1.5% of the collection (Table 1; Fig. 3). We also found two specimens at one site in the North Fork of the Spring River, and six individuals at a Shoal Creek site in Missouri (Table 1; Fig. 3). In the Cottonwood, Elk, Caney, and South Fork Rivers, only weathered shells of this species were noted (Table 1). Most *P. occidentalis* specimens were over seven years old. The youngest noted was a recently dead three-year-old specimen (41 x 20 x 9 mm) collected from a Fall

River site. Mean shell length for *P. occidentalis* in the Verdigris basin was 90.2 mm (SD = 20.74), whereas Spring River basin specimens were slightly larger (mean = 97.4 mm, SD = 16.17). Like *Lampsilis rafinesqueana*, *P. occidentalis* exhibited differences in habitat use among streams (Table 2); however, it was found predominantly in riffles.

Cyprogenia aberti was collected alive in only three streams, representing 0.2% of the total sample. In the Verdigris River, we collected 11 *C. aberti* at five sites, in the Fall River five specimens were found at four sites, and in the Spring River we collected 13 specimens at six sites (Table 1; Fig. 4). We also found one relic *C. aberti* valve from the Elk River (Table 1; Fig. 4), which represents a new stream record. Although *C. aberti* was documented in the Neosho River by both Call (1885a) and Scammon (1906), we were unable to find evidence of this species, either recent or weathered valves, in this stream. Only four of the *C. aberti* we collected were less than five years old, all measuring less than 45 mm in length; the smallest measured 34 x 26 x 16 mm. A Verdigris River site also yielded a young freshly dead specimen in exposed gravel, which measured 44 x 35 x 15 mm; we estimated this specimen to be three years old. Shell length of living specimens from the Spring, Fall, and Verdigris Rivers ranged 34 - 81 mm

Table 2. Observed habitat use [mean (SD)] by candidate mussels from Arkansas Basin streams in Kansas and Missouri.

Stream	N	Depth (cm)	Current speed (cm/s) at:		Substratum character (%):						Compaction	Siltation
			100% depth	60% depth	Mud	Sand	Gravel	Cobble	Boulder			
<i>Lampsilis rafinesqueana</i>												
Fall R.	34	34.1 (20.9)	12.4 (10.7)	13.2 (8.3)	0.7 (1.8)	11.7 (12.3)	48.4 (22.5)	37.6 (24.3)	1.5 (4.2)	1.2 (0.6)	1.3 (0.5)	
Verdigris R.	5	26.2 (18.9)	3.2 (4.6)	5.2 (7.3)	11.0 (16.3)	11.0 (5.7)	52.0 (18.2)	27.0 (17.2)	-	1.0 (0.0)	1.6 (0.5)	
Neosho R.	32	39.6 (22.2)	16.0 (13.8)	27.0 (25.4)	3.3 (6.6)	14.9 (13.7)	41.3 (20.0)	35.9 (24.6)	4.4 (14.4)	1.1 (0.4)	1.4 (0.5)	
Spring R.	258	33.0 (11.7)	43.5 (19.3)	72.4 (27.1)	1.0 (3.3)	16.4 (16.9)	74.3 (16.6)	-	-	1.0 (0.0)	0.2 (0.4)	
Shoal Cr.	20	59.4 (15.4)	20.4 (11.5)	42.2 (28.4)	0.3 (1.1)	17.1 (7.1)	74.5 (14.8)	8.3 (16.9)	-	0.9 (0.4)	0.1 (0.2)	
<i>Pychobranchus occidentalis</i>												
Fall R.	17	17.5 (12.8)	12.2 (11.9)	14.1 (10.6)	1.8 (3.3)	15.3 (12.2)	62.0 (19.5)	13.9 (12.1)	6.9 (20.7)	0.9 (0.2)	1.2 (0.6)	
Verdigris R.	9	19.0 (8.1)	13.2 (10.3)	18.6 (14.4)	2.6 (2.7)	15.3 (4.5)	73.2 (8.9)	8.9 (7.8)	-	1.0 (0.0)	1.3 (0.5)	
Spring R.	12	41.0 (17.7)	26.8 (19.8)	44.4 (27.9)	1.0 (1.8)	24.6 (25.2)	69.0 (24.1)	5.4 (6.6)	-	0.9 (0.3)	0.3 (0.5)	
Shoal Cr.	4	73.5 (4.0)	34.9 (7.1)	97.1 (6.4)	0.0 (0.0)	11.8 (2.4)	82.0 (3.6)	7.5 (5.0)	-	1.3 (0.3)	0.0 (0.0)	
<i>Cyprogenia aberti</i>												
Fall R.	5	29.6 (17.6)	8.4 (7.9)	16.8 (12.1)	0.2 (0.5)	14.2 (15.2)	18.4 (25.3)	45.2 (29.5)	22.0 (31.9)	1.0 (0.0)	1.2 (0.5)	
Verdigris R.	9	26.5 (26.)	17.1 (18.1)	20.9 (19.6)	4.1 (6.0)	12.6 (8.6)	7.3 (6.1)	75.1 (15.7)	-	0.8 (0.4)	1.5 (0.5)	
Spring R.	3	37.3 (10.7)	27.2 (17.0)	65 (35.8)	-	30.0 (35.0)	1.7 (2.9)	68.3 (33.3)	-	0.7 (0.6)	0.3 (0.6)	
<i>Quadrula cylindrica</i>												
Neosho R.	2	12.5 (13.4)	27.5 (16.3)	38.0 (31.1)	0.5 (0.7)	7.0 (4.2)	60.0 (8.5)	32.5 (3.5)	-	1.0 (0.0)	1.0 (0.0)	
Spring R.	5	44.2 (16.6)	23.8 (9.1)	56.2 (31.9)	-	20.0 (12.7)	80.0 (12.7)	-	-	0.9 (0.2)	0.2 (0.4)	

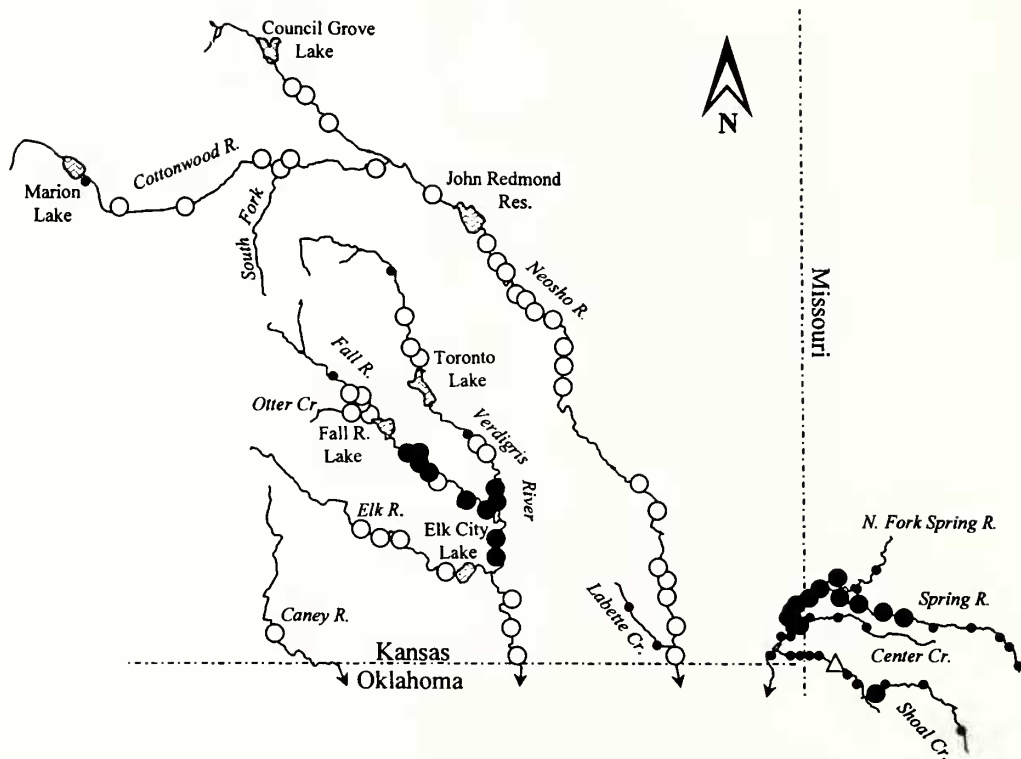


Fig. 3. Range map of *Prychobranchnus occidentalis* in the Neosho, Spring, and Verdigris River basins in southeastern Kansas and southwestern Missouri. Symbols as in Fig. 2.

(mean = 61.0 mm, SD = 13.40). *C. aberti* specimens collected in this study were generally confined to shallow riffles and runs in predominantly clean, moderately compacted gravel-sand substrata (Table 2).

Living representatives of *Quadrula cylindrica* were found in the Neosho and Spring Rivers (Table 1; Fig. 5), predominantly in shallow habitats with clean, moderately compacted gravel-sand substrata (Table 2). In the Neosho, we collected two living specimens from two sites (Table 1; Fig. 5), as well as two recently dead articulated specimens with desiccated softparts at one of these sites. Although freshly dead specimens of this species have been found in recent years in this stream (C. H. Cope, pers. comm.), these individuals are the first *Q. cylindrica* specimens reported alive from the Neosho River since 1912 (Isely, 1924). Relic *Q. cylindrica* valves were also found at nine additional Neosho River sites (Fig. 5). In the Spring River, we collected a total of five specimens at one Kansas and three Missouri sites (Table 1; Fig. 5). Relics were collected from one Shoal Creek site in Missouri, which represents the first evidence of this species in Shoal Creek. New stream records for *Q. cylindrica* were also made for the Fall and Cottonwood Rivers, with relic valves collected at two sites in each of these streams. Although Isely (1924) reported living *Q. cylindrica* in the Verdigris River in 1912, we

found only relic valves of the species at eight of 14 sites (Fig. 5).

We estimated that three *Quadrula cylindrica* specimens from the Neosho River (two recently dead and one alive) were in their sixth year of growth (78, 86, and 87 mm long); an additional living specimen was estimated to be in excess of ten years old (113 mm long). A rather large specimen (recently dead valve) of this species, which measured 127 mm in length, was also recovered at one of these sites. In the Spring River, *Q. cylindrica* specimens ranged 74 - 109 mm in length (mean = 93.0 mm; SD = 12.71).

Only one *Alasmidonta marginata*, measuring 73 x 38 x 30 mm, was collected during the study, at a Kansas Spring River site (Table 1). It was found in riffle habitat with current speeds of 72 and 33 cm/s (60 and 100% depth, respectively) at 54 cm depth in predominantly cobble substratum (6% sand, 15% gravel, and 79% cobble). Weathered shells of this species were recovered at two additional Spring River sites in Kansas; one weathered valve was found at a Shoal Creek site in Missouri, the first account of this species in that stream.

Although *Toxolasma lividus* was not initially targeted in this study, we found three living individuals at one site in Shoal Creek in Missouri, as well as dead shells at three additional Shoal Creek sites (Table 1). The three living speci-

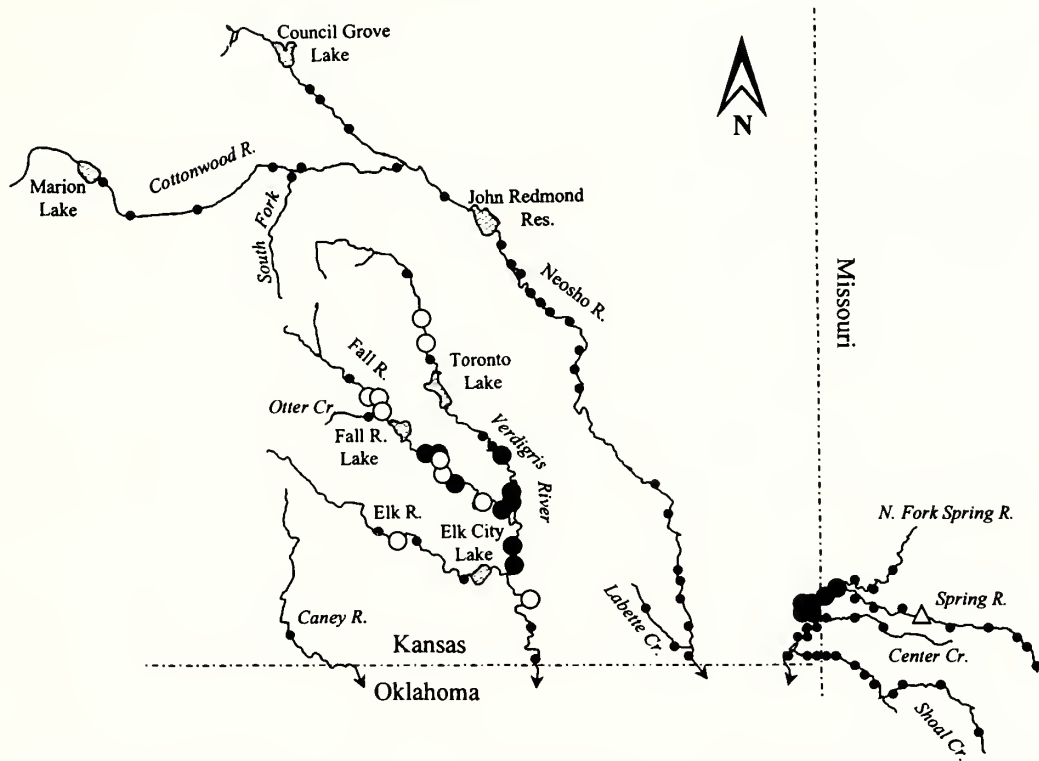


Fig. 4. Range map of *Cyprogenia aberti* in the Neosho, Spring, and Verdigris River basins in southeastern Kansas and southwestern Missouri. Symbols as in Fig. 2.

mens were found in a shallow backwater pool, which consisted of silty sediments with no detectable current.

DISCUSSION

Habitat descriptions for freshwater mussels have often been generalized (Gordon and Layzer, 1989). For example, *Quadrula cylindrica* occurring in medium to large streams is cited as preferring sand-gravel substrata in 6-10 feet of water (Parmalee, 1967; Cummings and Mayer, 1992) with a detectable current (Parmalee, 1967). However, in smaller streams the species is considered a riffle species, being most often found near shore in cobble substratum with a slack current (Stansbery, 1974) or, as Gordon and Layzer (1989) reported, in close proximity to the swiftest flows. Anecdotal descriptions of habitat use by *Ptychobranhus occidentalis* are gravel substratum in riffles with depths between 2.5 and 75 cm in slow to moderate current (Buchanan, 1980; Oesch, 1984); Gordon and Layzer (1989) stated that two congeners, *P. fasciolaris* (Rafinesque, 1820) and *P. subtentum* (Say, 1825), seem to prefer shallow riffles in moderate to swift currents. Habitat use by *Cyprogenia aberti* is described as shallow water (7-45 cm), with mud, sand, and gravel substrata (Murray and Leonard, 1962; Buchanan, 1980; Oesch, 1984).

Alasmidonta marginata is reported to prefer riffles in cobble-gravel and gravel-sand substrata in medium to large rivers (Clarke and Berg, 1959; Clarke, 1981; Cummings and Mayer, 1992), with a preference for moderate to swift currents (Clarke and Berg, 1959; Gordon and Layzer, 1989). Oesch (1984) described the habitat use of *Lampsilis rafinesqueana* in Missouri as shallow water with a moderate current in fine to medium gravel.

More detailed habitat descriptions for unionids are difficult because of broad microhabitat tolerances (Strayer, 1981; Kat, 1982; Gordon and Layzer, 1989; Holland-Bartels, 1990; Strayer and Ralley, 1993; Strayer *et al.*, 1994), and because of site-specific preferences (Strayer, 1981) due to macro-scale variation (*e. g.* hydrologic variability) among sites (Strayer and Ralley, 1993). Habitat use by mussels collected in the present study was also variable when compared among different streams (Table 2), which made it difficult to extrapolate habitat suitability indices from one stream to another. Habitat use on a broader scale, however, was more predictable; that is, mussels were most often found in shallow riffles and runs at depths less than one meter, with stable and moderately compacted substratum, predominantly gravel, with a minimum of silt. Examination of deeper, more silt-laden habitats (*i. e.* pools) revealed a decrease in species richness and abundance of

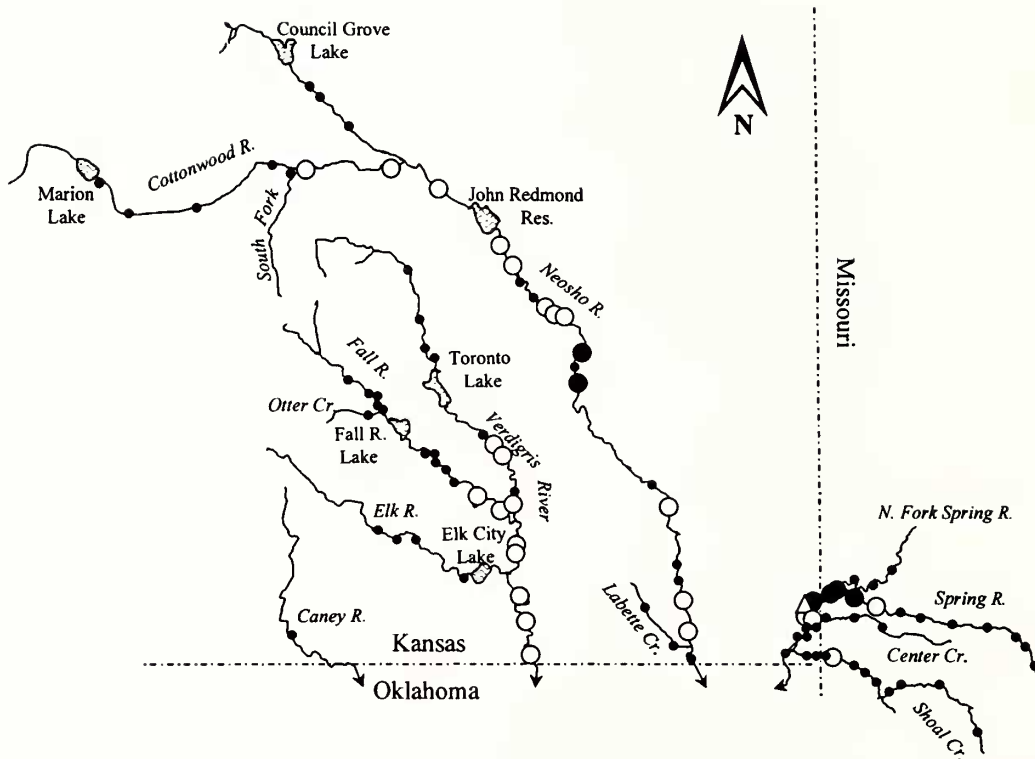


Fig. 5. Range map of *Quadrula cylindrica* in the Neosho, Spring, and Verdigris River basins in southeastern Kansas and southwestern Missouri. Symbols as in Fig. 2.

unionids, including the absence of candidate species. Sites that were unstable (*i. e.* loose, shifting substrata) were especially low in unionid numbers.

Of the five species targeted in this study, habitat use by *Lampsilis rafinesqueana* was especially intriguing. In the Neosho, Verdigris, Spring, and North Fork Spring Rivers, *L. rafinesqueana* was found most often in riffle habitat, usually in a swift current. However, in Shoal Creek, the species was often found in habitats near shore or out of the strongest current. Mather (1990) and C. C. Vaughn (pers. comm.) found a similar trend in another Ozarkian stream, the Illinois River in Oklahoma, and described the habitat most often associated with *L. rafinesqueana* in this stream as backwater areas. The rarity of *L. rafinesqueana* in mid-channel flows in Shoal Creek might be due to greater disruptions of substratum, especially during spates, than in other streams. Despite *L. rafinesqueana*'s apparent inability to colonize extremely unstable habitats, this species seemed more adapted to unstable habitats than most other unionids. We observed that individuals of *L. rafinesqueana* in the Spring River and Shoal Creek often had their foot well extended into the substratum, especially in loose gravel. Kat (1982) similarly noted that *Elliptio complanata* (Lightfoot, 1786) used its foot to maintain a viable position in unstable habitats (*i. e.* soupy mud). Foot

extension of *L. rafinesqueana* was seldom observed, however, in prairie streams of the Neosho and Verdigris basins and in the North Fork Spring River. Foot anchoring by *L. rafinesqueana* in the Spring River basin was probably due to swifter average current speeds in the Spring River basin versus the Neosho and Verdigris River basins (Table 2), and because substrata in the Spring River and Shoal Creek were less compacted than those in the prairie streams mentioned.

Lampsilis rafinesqueana has apparently become extirpated from six Kansas streams: the Elk, Caney, Cottonwood, and South Fork of the Cottonwood Rivers, and Shoal and Middle Creeks (Cope, 1979, 1985; Metcalf, 1980; Obermeyer, 1996b; Obermeyer *et al.*, 1997), and currently remains in the Verdigris, Fall, Neosho, and Spring Rivers (Cope, 1979, 1983, 1985; Miller, 1993; Obermeyer *et al.*, 1995; 1997) (Fig. 2). In addition to its range decline in Kansas, *L. rafinesqueana* seems to have become less abundant (Obermeyer *et al.*, 1997). It is presently listed in Kansas as endangered. In Missouri, *L. rafinesqueana* is confined to the Spring and Elk River basins (Gordon and Brown, 1980; Johnson, 1980; Oesch, 1984; Clarke and Obermeyer, 1996), and is state-listed as rare (Anonymous, 1994). Despite the decline of *L. rafinesqueana* in Kansas, the relative abundance of this species could have increased in the Spring River since Branson's (1967) survey. For

example, Branson collected only 15 "muckets" at one of our Spring River sites in Kansas, whereas we found 112 living *L. rafinesqueana* [Note: His identifications of *Actinonaias ligamentina* (Barnes, 1823) were likely *L. rafinesqueana*]. Presently, the species is probably more abundant in the Spring River from Carthage, Missouri, to near the confluence of Center Creek, Kansas, than anywhere else throughout its range. Although *L. rafinesqueana* appears to remain within most of its historic range in Missouri, Branson (1967) recovered the species at sites farther upstream in both the Spring River and Shoal Creek, perhaps indicating a slight decrease in range. In the Kansas portion of the Spring River, *L. rafinesqueana*, as well as most other riverine mussel species, is apparently extirpated downstream from Turkey Creek (Fig. 2). Although *L. rafinesqueana* was previously reported as absent in the Spring River downstream from the confluence of Center Creek (Cope, 1985; Stewart, 1992; Obermeyer et al., 1995), we collected this species at two riffle sites immediately downstream from Center Creek, which may indicate improving stream conditions.

Lampsilis rafinesqueana is a bradytic breeder (Barnhart and Roberts, 1997), and females, like other lampsilines, attract potential hosts with a mantle lure (Johnson, 1980; Oesch, 1984; Barnhart and Roberts, 1997), with July and August being the period of most frequent mantle display (B. K. Obermeyer, pers. obs.). Two potential hosts have been identified for *L. rafinesqueana*: smallmouth bass (*Micropterus dolomieu* Lacépède, 1802) and largemouth bass [*M. salmoides* (Lacépède, 1802)] (Barnhart and Roberts, 1997); M. C. Barnhart (pers. comm.) suspects that spotted bass [*M. punctulatus* (Rafinesque, 1819)] would also serve as a host, although this species has not been tested.

Ptychobranthus occidentalis has experienced the largest reduction in range in Kansas of the five candidate species targeted in this study (Obermeyer et al., 1997). Ten Kansas streams have historic records for this species: the Cottonwood, South Fork of the Cottonwood, Elk, Fall, Caney, Neosho, Spring, and Verdigris Rivers, and Otter (Greenwood County) and Cedar (Chase County) Creeks (Popenoe, 1885; Call, 1885c, 1885d, 1886; Scammon, 1906; Isely, 1924; Cope, 1979, 1985; Metcalf, 1980; Obermeyer et al., 1995, 1997). However, extant representatives have been recovered recently from only four Kansas streams: the Neosho, Spring, Fall, and Verdigris Rivers (Branson, 1966a, 1967; Frazier, 1977; Liechti and Huggins, 1977; Schuster, 1979; Schuster and DuBois, 1979; Cope, 1979, 1983, 1985; Miller, 1993; Obermeyer et al., 1995, 1997). Furthermore, *P. occidentalis* might have recently become extirpated from the Neosho River (Obermeyer et al., 1995). In the Spring River basin, *P. occidentalis* was uncommon. This observation agrees with the contention of Buchanan (1980) and Oesch (1984) that *P. occidentalis*,

although widely distributed in the southern half of Missouri, is uncommon at any one locale. Presently, *P. occidentalis* is listed as threatened in Kansas and as a watch species (i.e. a species of concern) in Missouri (Anonymous, 1994).

Ptychobranthus occidentalis is a bradytic breeder (Johnson, 1980; Barnhart and Roberts, 1997) that releases mimetic larval packets from pleated marsupial gills in early spring (Barnhart and Roberts, 1997). The orangethroat [*Etheostoma spectabile* (Agassiz, 1854)], greenside (*E. blennioides* Rafinesque, 1819), yoke (*E. juliae* Meek, 1891), and rainbow darter (*E. caeruleum* Storer, 1845) have been identified as potential hosts (Barnhart and Roberts, 1997). Of these four species, only two species are found in the study area; the greenside darter is found in the Spring River basin, whereas the orangethroat darter is found throughout the study area (Pflieger, 1975; Cross and Collins, 1995).

Cyrogenia aberti occurred historically in Kansas in the Fall, Elk, Verdigris, Neosho, Spring Rivers (Popenoe, 1885; Call, 1885a, b, 1886, 1887a; Scammon, 1906; Murray and Leonard, 1962; Obermeyer et al., 1995, 1997); however, it has been found recently in only the Verdigris, Fall, and Spring Rivers (Branson, 1966b; Liechti and Huggins, 1977; Cope, 1979, 1985; Miller, 1993; Obermeyer et al., 1995, 1997), and is considered rare with a patchy distribution (Obermeyer et al., 1997). Oesch (1984) and Harris and Gordon (1987) reported that in Ozarkian streams of Missouri and Arkansas, *C. aberti* was locally abundant, especially in the Spring (White River system) and Caddo (Ouachita River system) Rivers in Arkansas (Harris and Gordon, 1987). However, we found the species uncommon in the Spring River basin. *C. aberti* is presently listed as endangered in Kansas and as rare in Missouri (Anonymous, 1994).

Gravid females of *Cyrogenia aberti* have been found in all stages of reproductive development throughout the year (Call, 1887b); however, Chamberlain (1934) observed that the species released conglutinates in late winter, and M.C. Barnhart (pers. comm.) observed the periodic release of conglutinates during winter and spring months. Preliminary findings by M. C. Barnhart (pers. comm.) indicate that, from a total of 24 species infected, the banded sculpin [*Cottus carolinae* (Gill, 1861)], log perch [*Percina caprodes* (Rafinesque, 1818)], and fantail darter (*Etheostoma flabellare* Rafinesque, 1819) are suitable hosts, based on Spring River *C. aberti* specimens. Another cited host for *C. aberti* is the goldfish [*Carassius auratus* (Linnaeus, 1758)] (Watters, 1994), based on Chamberlain (1934); however, although glochidial cysts on goldfish were noted for up to five hours following that fish's ingestion of *C. aberti* conglutinates, subsequent examinations of glochidial cysts (i. e. after 5 h) were not made to determine

host suitability.

Oesch (1984) reported that *Quadrula cylindrica* is restricted in Missouri to the Black, St. Francis, and Spring Rivers; it also occurred historically in Center Creek (Utterback, 1915) as well as in Shoal Creek (Clarke and Obermeyer, 1996). In Kansas, Obermeyer *et al.* (1997) stated that *Q. cylindrica*'s continued persistence in the state is questionable, with extant representatives limited to a few locales in the Spring and Neosho Rivers (Cope, 1985; Obermeyer *et al.*, 1997). Its current distribution contrasts greatly with its past presence in the Neosho, Cottonwood, Spring, Verdigris, and Fall Rivers as well as in Shoal Creek (Popenoe, 1885; Call, 1885b, d; Scammon, 1906; Isely, 1924; Obermeyer *et al.*, 1997). Clarke and Obermeyer (1996) remarked that the species has exhibited a similar trend of decline throughout most of its range in eastern North America. *Q. cylindrica* is presently listed as endangered in both Kansas and Missouri.

Knowledge of the reproductive biology of *Quadrula cylindrica* is based largely on Tennessee populations of *Q. c. strigillata*, except for brief breeding records by Utterback (1915) and Ortmann (1919). Yeager and Neves (1986) found *Q. c. strigillata* to be tachytictic, with the bigeye chub [*Notropis amblops* (Rafinesque, 1820)], spotfin shiner [*Cyprinella spiloptera* (Cope, 1868)], and whitetail shiner [*C. galactura* (Cope, 1868)] potential hosts based on artificial infestations. Although differences between *Q. c. cylindrica* and *Q. c. strigillata* could be due to phenotypic plasticity (Gordon and Layzer, 1989; Clarke and Obermeyer, 1996), it is possible that host specificity varies between eastern populations, especially of *Q. c. strigillata*, and those further west, such as in Kansas and Missouri. Further evidence of host differences is suspected because in the Neosho River, where small populations of this species remain, suitable hosts identified by Yeager and Neves (1986) are believed to be absent (Cross, 1967; F. B. Cross, pers. comm.).

Oesch (1984) described *Alasmidonta marginata* as being widely distributed in the southern half of Missouri, but noted it is uncommon at any one locale. *A. marginata* was first documented in Kansas by Branson (1966a), who found three living specimens in the Spring River in 1964. Although additional specimens have since been collected in the Spring River (Obermeyer *et al.*, 1995), the only other stream record for *A. marginata* in Kansas is from the Marais des Cygnes River in east-central Kansas, based on a recently dead specimen in Franklin County collected in 1983 (Distler and Bleam, 1987) and a relic valve found in Osage County (Obermeyer, 1996b). The recovery of only one living *A. marginata* and the rarity of fresh shell material in the present study raises concern for the species because earlier surveyors (Branson, 1967; Cope, 1985) found the species in the Spring River in Kansas more fre-

quently and at more sites. It is listed in Kansas as endangered, but is not currently listed in Missouri.

Five potential hosts have been identified for *Alasmidonta marginata* (*vide* Howard and Anson, 1923), which is a bradytictic breeder (Ortmann, 1919; Oesch, 1984; Watters, 1994). These are the northern hog sucker [*Hypentelium nigricans* (Lesueur, 1817)], rock bass [*Ambloplites rupestris* (Rafinesque, 1817)], shorthead redhorse [*Moxostoma macrolepidotum* (Lesueur, 1817)], warmouth [*Lepomis gulosus* (Cuvier, 1829)], and white sucker [*Catostomus commersoni* (Lacépède, 1803)], all of which occur in the Spring River basin (Pflieger, 1975; Cross and Collins, 1995).

CONCLUSIONS

Clarke and Obermeyer (1996) recommended federal listing status for four of the five species targeted in this study; that is, all except *Alasmidonta marginata*, which is on the western edge of its range in the study area and is widely distributed throughout much of eastern North America (Clarke, 1981). Clarke and Obermeyer (1996) stressed the need for habitat conservation as the key element for future protection of these species, and regarded preservation of the Spring River mussel fauna a top priority because of its diverse mussel assemblage. Furthermore, they considered the Spring River a possible refuge from the impending threat of *Dreissena polymorpha* (Pallas, 1771) (French, 1990; Ludyanskiy *et al.*, 1993) because of the rarity of headwater impoundments, which can function as upstream sources for *Dreissena veligers* (McMahon, 1991). They also regarded the Spring River an important refuge because of its tolerance of droughts due to spring-fed flows. We agree that the Spring River is an important resource to conserve, and believe that basin-wide recovery/protection plans [*e. g.* U. S. Fish and Wildlife Service (1994)] should be considered to help protect remaining mussel assemblages in not the Spring River, but in the Neosho, Verdigris, and Fall River basins as well. Because populations of some of these unionids examined in this study could be ecologically distinct despite exhibiting similar shell morphology with other populations (*e. g.* possible differences in host specificity for *Quadrula cylindrica*), unique biological entities are perhaps being overlooked. Therefore, we believe it is important to identify and protect these disjunct and/or distinct populations. We also recommend additional testing of potential fish hosts for these and other species, perhaps on a drainage-by-drainage basis.

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